Data Collection on Intergeneric Hybrids and Basic Types: BRYOPHYTA s. l.

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„BRYOPHYTA s. l.“

mosses, hornworts and liverworts

= Laubmoose, Hornmoose und Lebermoose

Systematics according to en.wikipedia 2025. The taxonomy has been intensively changed in the last years! What formerly had the rank of a division Bryophyta s. l. is now divided into 3 divisions:
Anthocerotophyta (hornworts): 2 classes, 5 orders, 5 families, 214 species
Marchantiophyta (liverworts): 3 classes, 15 orders, 46 families, 9000 species
Bryophyta s. str. (mosses): 8 classes, 45 orders, 127 families, 12000 species

Hybrids are only known in division Bryophyta s. str.

In all mosses the diplophase is restricted to the sporogon which often lacks conspicuous differences between related taxa. Therefore it is rather difficult to detect hybrids. See the literature below, e. g. Natcheva & Cronberg 2004, where all known (natural) interspecific and intergeneric hybrids are listed.

Abbreviations:

° = taxa actually not accepted in the rank of a genus, e. g. *Cerasus*° (= *Prunus* p. p.)
10: 50 etc. The numbers behind the names of families etc. refer to extant genera and species
IS = interspecific hybrid. **IG** = intergeneric hybrid. **IST** = intersubtribal hybrid.
IT = intertribal hybrid. **ISF** = intersubfamilial hybrid. **IF** = interfamilial hybrid.
EC = embryo culture or ovule culture
SO = somatic hybrid by cell fusion; normally these hybrids are asymmetric
AS = asymmetric hybrids, they do not equally express maternal and paternal features
HY = assumed intergeneric hybridogeneous origin of a taxon.
nat. hyb. = natural hybrid **art. hyb.** = artificial hybrid

Colours within the crosses:

Red letters: intergeneric hybrids (incl. former IG).
Violet letters: multigeneric = plurigeneric hybrids.
Gray letters: hybridity unconfirmed or erroneous.
Green letters: notes on tribes, subfamilies etc. involved in the hybridization.

Yellow shaded: Notes concerning basic types.

General references on Bryophyta:

Anderson LE (1980) Cytology and reproductive biology of mosses. p. 37–76 in: Taylor RJ & Leviton AE (eds.) The mosses of North America. San Francisco: Pacific Div. Amer. Assoc. Adv. Sciences.

Ignatov MS et al. (2018) Hybridization in mosses, how distant it can be. Zhurnal Obshchei Biologii (= J. Gen. Biol.) 79 (2), 159–166. [In Russian] https://elementy.ru/genbio/abstracts/551/Hybridization_in_mosses_how_distant_it_can_be Not yet analyzed. In the summary the existence of interfamily hybrids is mentioned

Klinggraeff H von (1889) Über die Bastarde bei Farnen und Moosen. Schriften Naturforsch. Ges. Danzig N. F. 7 (2), 172–178.

Natcheva R & Cronberg N (2004) What do we know about hybridization among bryophytes in nature? Can. J. Bot. 82, 1687–1704. Including putative gametophytic hybrids, not listed here

Sanio C (1887) Bryologische Fragmente. III. Hedwigia 26, 194–214.

Timm R (1927) Über Moosbastarde, insbesondere über die Kreuzungen und Mittelformen zwischen *Pogonatum aloides* (Hedw.) PB. und *nanum* (Schreb.) PB. Hedwigia 67, 1–44.

Wyatt R et al. (1988) Hybrid origin of polyploid moss *Plagiomnium medium*. p. 22 in: Sixth Meeting Central East European Bryol. Working Group (Liblice, Czechoslovakia).

Division
BRYOPHYTA s. str. = MUSCI

8 classes, 45 orders, 127 families, 12000 species

mosses = Laubmoose

8 classes:
Andreaeopsida: 1 family, 1 genus, 100 species
Andreaeobryopsida: 1 family, 1 genus, 1 species
Bryopsida: 7 subclasses, 37 orders, 118 families, 11500 species
Oedipodiopsida: 1 family, 1 genus, 1 species
Polytrichopsida: 1 family, 20 genera, 220 species
Sphagnopsida: 1–2 extant orders, 2–3 families, 4 genera, 150–300 species
Takakiopsida: 1 family, 1 genus, 2 species
Tetraphidopsida: 1 family, 2 genera, 4 species

Arrangement of families according to the order

Bryales 6 families (class Bryopsida, subclass Bryidae)

Bryales: Bryaceae 10: 660

IS: *Bryum 6 IS, Meesia 1 IS, Pogonatum 1 IS* (see Natcheva & Cronberg 2004)

Brachymenium × *Bryum* Ochi 1954 (*Bra. exile* × *Bry. argenteum*)
Bryum × *Pohlia* (nat. hyb.) Ochi 1961 (*B. pallescens* × *P. crudoides*) v. Wettstein 1932 (*B. bicolor* × *P. melanodon*)

References on Bryaceae:
Ochi H (1954) Notes on the mosses of Bryaceae in Japan, II. Intergeneric hybrid sporogone between *Bryum argenteum* var. *lanatum* (Palis) Bry. eur., and *Brachymenium exile*. J. Jpn. Bot. 29, 49–51.
Ochi H (1961) Mosses of the Bryaceae in Japan and the adjacent regions, suppl. II. Possibly natural intergeneric hybrid (*Bryum pallescens* Schl. × *Pohlia crudoides* Broth.). Nikobia (Hiroshima) 2 (3), 179–184.
Wettstein F von (1932) Genetik. In Manual of bryology. Ed. by F. Verdoorn. Hague, The Netherlands. pp. 233–272.

Dicranales 20 families (class Bryopdsida, subclass Dicranidae)

Dicranales: Bruchiaceae 3–5: 120

Bruchia, Eobruchia, [Pringleella], Trematodon

Bruchia microspora × *Trematodon longicollis* (nat. hyb.) Rushing & Snider 1985, Natcheva & Cronberg 2004

References on Bruchiaceae:

Rushing AE & Snider JA (1985) A natural hybrid between *Bruchia microspora* Nog. and *Trematodon longicollis* Michx. Monogr. Syst. Bot. Missouri Bot. Garden 11, 121–132.

Dicranales: Dicranaceae 24: 410

IS: *Campylopus flexuosus* × *C. fragilis* Natcheva & Cronberg 2004, *Dicranella cerviculata* × *D. heteromalla* Natcheva & Cronberg 2004

Dicranales: Ditrichaceae 25: 140

IS: *Astomopsis amblyocalyx* × *A. exserata* (Natcheva & Cronberg 2004)

Ditrichum × *Pleuridium* (→ × *Pleuriditrichum*)(nat. hyb., *D. pallidum* × *P. acuminatum, palustre; D. subulatum* × *P. subulatum*) Limpricht 1890 (Austria, Steiermark), Venturi 1881 (Portugal, Oporto), Andrews & Hermann 1959, Futschig & Kellner 1959 (Germany), Andrews 1960, Anderson & Snider 1982, Natcheva & Cronberg 2004

References on Ditrichaceae:

Anderson LE & Snider JA (1982) Cytological and genetic barriers in mosses. J. Hattori Bot. Lab. (Nichinan) 52, 241–254.

Andrews AL (1960) Taxonomic notes. XV. The reciprocal hybrid of *Ditrichum-Pleuridium*. Bryologist 63, 179–181.

Andrews AL & Hermann FJ (1959) A natural hybrid in the Ditrichaceae. Bryologist 62, 119–122.

Futschig J & Kellner K (1959) Über Moosbastarde am natürlichen Standort. 1. Mitteilung: Ein neuer Bastard, *Pleuridium subulatum* (Schreb.) Lind. × *Ditrichum pallidum* (Schreb.) Hampe. Hess. Florist. Briefe 8 (93), 1–2.

Limpricht KG (1890) Die Laubmoose Deutschlands, Oesterreichs und der Schweiz. I. Leipzig: Kummer.

Venturi G von (1881) Une mousse hybride. Revue Bryol. 1881, 20–22.

Funariales 1family (class Bryopsida, subclass Funariidae)

Funariales: Funariaceae 14: 300

2 subfamilies:
Funarioideae 12: 395 *Entosthodon 85, Funaria 80, Physcomitrella 2, Physcomitrium 65, ...*
Pyramiduloideae 2: 5: *Goniomitrium 4, Pyramidula 1*

For compilations of hybrids and discussions, see von Wettstein 1924 a, b, 1925, 1940, Bauer & Brosig 1959, Fife 1985, Adler 1993, Natcheva & Cronberg 2004

IS: *Funaria 1 IS* (*F. hygrometrica* × *F. muehlenbergi*, art. hyb. von Wettstein 1924, 1925), *Physcomitrium 2 IS* (*P. eurystomum* × *P. pyriforme*, art. hyb. von Wettstein 1924, 1925), *P. immersum* × *P. turbinatum* nat. hyb. Andrews 1942)

Probable basic type **family Funariaceae** (Adler 1993). But the number of 4 intergeneric hybrids is rather small.

Entosthodon × *Funaria* (nat. hyb.) von Wettstein 1924 a, b, 1925 (*E. fascicularis* × *F. hygrometrica*), Natcheva & Cronberg 2004
Funaria × *Physcomitrella* (→ × *Funariophyscomitrella* F. Wettst.) (nat. + art. hyb., *F. hygrometrica* × *P. patens*) von Wettstein 1924 a, b, 1925, Natcheva & Cronberg 2004
Funaria hygrometrica × *Physcomitrium pyriforme* Bayrhoffer 1849, von Wettstein 1924 a, b, 1925, Natcheva & Cronberg 2004
Physcomitrella × *Physcomitrium* (*P. patens* × *P. sphaericum, turbinatum* nat. hyb.) Amann 1893 (Switzerland), Andrews 1942, McDaniel et al. 2010, Natcheva & Cronberg 2004

References on Funariaceae:

Adler M (1993) Merkmalsausbildung und Hybridisierung bei Funariaceen (Bryophyta, Musci). p. 67–70 in Scherer S (ed.) Typen des Lebens. Berlin: Pascal.
Andrews AL (1942) Taxonomic notes II. Another natural hybrid in the Funariaceae. Bryologist 45, 179–181.
Bauer L & Brosig M (1959) Zur Kenntnis reziproker Kreuzungen von Funariaceen. I. Die Bastarde *Funaria hygrometrica* × *Physcomitrium acuminatum* und reziprok. Z. Vererbungslehre 90, 400–408.
Bayrhoffer J (1849) Übersicht der Moose, Lebermoose und Flechten des Taunus. Jahrb. Nassau. Ver. Naturkd. 5, 101.
McDaniel SF, Mark von Stackelberg M, Sandra Richardt S, Ralph S. Quatrano RS, Ralf Reski R & and Stefan A. Rensing SA (2010) The speciation ishtory of the *Physcomitrium - Physcomitrella* species complex. Evolution 64, 217–231.

Patel N, Medina R et al. (2023) Frequent allopolyploidy with distant progenitors in the moss genera *Physcomitrium* and *Entosthodon* (Funariaceae) identified via subgenome phasing of targeted nuclear genes. Evolution 77, 2561–2575. https://biodiversity.uconn.edu/2023/12/02/new-publication-on-bryophytes-2/
Wettstein F von (1924a) Morphologie und Physiologie des Formwechsels der Moose auf genetischer Grundlage I. Z. Indukt. Abstammungs- Vererbungslehre 33, 1–236.
Wettstein F von (1924 b) Gattungskreuzungen bei Moosen. Z. Indukt. Abstammungs-Vererbungslehre 33, 253–257.
Wettstein F von (1925) Genetische Untersuchungen an Moosen (Musci und Hepaticae). Bibliographia Genetica (The Hague) 1, 1–38.
Wettstein F von (1940) Experimentelle Untersuchungen zum Artbildungsproblem II. Zur Frage der Polyploidie als Artbildungsfaktor. Ber. Deutsch. Bot. Ges. 58, 374–388.

Grimmiales 4 families (class Bryopsida, subclass Dicranidae)

Grimmiales: Grimmiaceae 10: 330

IS: *Grimmia 4 IS, Racomitrium 1 IS (R. heterostichum* × *macrocarpum* Natcheva & Cronberg 2004)

Orthotrichales 1 family (class Bryopsida, subclass Bryidae)

Orthotrichales: Orthotrichaceae 32

IS: *Orthotrichum 1 IS* (see references)

References on Orthotrichaceae:

Hedderson TA (1986) A naturally occurring moss hybrid between *Orthotrichum gymnostomum* and *O. obtusifolium* from Newfoundland, Canada. Bryologist 89, 165–167.

Polytrichales 1 family (class Polytrichopsida)

Polytrichales: Polytrichaceae 20: 220 + some extinct genera

Pogonatum × *Polytrichastrum* Derda et al. 2000 **HY** (arguments for the intergeneric hybridogeneous origin of some species of *Polytrichastrum* are given)
Polytrichum × *Polytrichastrum* Derda et al. 2000 **HY** (arguments for the intergeneric hybridogeneous origin of some species of *Polytrichastrum* are given)

References on Polytrichaceae:

Derda GS, Wyatt R, Derda GS & Wyatt R (2000) Isozyme evidence regarding the origins of three allopolyploid species of *Polytrichastrum* (Polytrichaceae, Bryophyta). Plant Syst. Evol. 220, 37–53.

Pottiales 4 or more families (class Bryopsida, subclass Dicranidae)

Pottiales: Pottiaceae 83: 1500

IS: *Pottia 2 IS, Weissia 3 IS* (see Natcheva & Cronberg 2004)

Phascum cuspidatum × *Pottia intermedia* Ulychna 1977, Natcheva & Cronberg 2004
Tortella (*„Trichostomum"*) *flavovirens* × *Weissia longifolia* (*„crispa"*) Nicholson 1910, Natcheva & Cronberg 2004
Weissia (*Astomum*°) *ludovicianum, muehlenbergianum* × *Weissia controversa* **IS** (now interspecific) (nat. hyb.) Nicholson 1931, Khanna 1960, Reese & Lemmon 1965, Williams 1966, Anderson & Lemmon 1972

References on Pottiaceae:

Anderson LE & Lemmon BE (1972) Cytological studies of natural hybrids and their parental species in the moss genera, *Astomum* and *Weissia*. Ann. Missouri Bot. Garden 59, 382–416. http://biostor.org/reference/11983
Nicholson WE (1910) A new hybrid moss. Rev. Bryol. 37, 23–24.
Nicholson WE (1931) Hybridity among the bryophytes. Revue Bryol. N. S. 4, 138–140.
Khanna KR (1960) Differential evolutionary activity in bryophytes. Evolution 18, 652–670.
Reese WD & Lemmon BE (1965) A natural hybrid between *Weissia* and *Astomum* and notes on the nomenclature of the North American species of *Astomum*. Bryologist 68, 277–283.
Ulychna KO (1977) Hybrid sporogones in *Phascum cuspidatum*, Pottiaceae, Musci. Ukr. Bot. Zh. 34, 155–158.
Williams C (1966) A natural hybrid in the genus *Weissia*. Bryologist 69, 361–365.

Sphagnales 3 families (class Sphagnopsida)

Sphagnales: Sphagnaceae 2: 200

IS: see the references below

Possibly basic type **family (or order) Sphagnaceae** due its isolated position.
Attention: Some authors distinguish 2–3 families in this order.

References on Sphagnaceae:

Cronberg N & Natcheva R (2002) Hybridization between the peat mosses, *Sphagnum capillifolium* and *S. quinquefarium* (Sphagnaceae, Bryophyta) as inferred by morphological characters and isozyme markers. Plant Systematics and Evolution 234, 53–70.

Flatberg KI (1988) *Sphagnum angustifolium* (Russ.) C. Jens. × *S. pulchrum* (Braithw.) Warnst., a gametophytic hybrid. Lindbergia 14, 4–7.

Splachnales 2 families (class Bryopsida, subclass Bryidae)

Splachnales: Splachnaceae 6: 70

2 subfamilies:
Splachnoideae 4 *Aplodon 1, Splachnum 11, Tetraplodon 9, Voitia 2.*
Tayloroideae 2 *Moseniella 2, Tayloria 47.*

Tetraplodon mnioides × *Voitia hyperborea* (nat. hyb.) v. Wettstein 1932

References on Splachnaceae:

Wettstein F von (1932) Genetik. In: F. Verdoorn (ed.) Manual of bryology. Hague, The Netherlands, pp. 233–272.